

Phycology and the algae

- Phycology or algology is the study of the algae.
- The word **phycology** is derived from the Greek word *phykos*, which means "seaweed" or algae and logos which means science, i.e. the science of algae.
- Thus, Phycology or algology is the study of the algae (singular, alga). This discipline deals with the morphology, taxonomy, phylogeny, biology, and ecology of algae in all ecosystem.
- **WHAT ARE THE ALGAE?**
- The algae are **thallophytes** (plants lacking roots, stems, and leaves) that have chlorophyll *a* as their primary photosynthetic pigment and lack a sterile covering of cells around the reproductive cells.
- This definition encompasses a number of plant forms that are not necessarily closely related, for example, the cyanobacteria which are closer in evolution to the bacteria than to the rest of the algae.

Basic characteristics of the algae

Phycology
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Then, how to distinguish algae from plants?

The answer is quite easy because the similarities between algae and plants are much fewer than their differences.

- **Plants** show a very high degree of differentiation, with roots, leaves, stems, and xylem/phloem vascular network.
- Their reproductive organs are surrounded by a jacket of sterile cells.
- They have a multicellular diploid embryo stage that remains developmentally and nutritionally dependent on the parental gametophyte for a significant period (and hence the name embryophytes is given to plants).
- They have tissue-generating parenchymatous meristems at the shoot and root apices, producing tissues that differentiate in a wide variety of shapes.
- Moreover, all plants have a digenetic life cycle with an alternation between a haploid gametophyte and a diploid sporophyte.

- The term algae has no formal taxonomic standing. It is routinely used to indicate a polyphyletic (i.e., including organisms that do not share a common origin, but follow multiple and independent evolutionary lines), noncohesive, and artificial assemblage of O₂-evolving, photosynthetic organisms (with several exceptions of colorless members undoubtedly related to pigmented forms).
- According to this definition, plants could be considered an algal division.
- Algae and plants produce the same storage compounds, use similar defense strategies against predators and parasites, and a strong morphological similarity exists between some algae and plants.

The profound diversity of

- **size** ranging from picoplankton only 0.2–2.0 μm in diameter to giant kelps with fronds up to 60 m in length,
 - **ecology** and colonized habitats,
 - **cellular structure**,
 - **levels of organization** and morphology,
 - **pigments** for photosynthesis,
 - **reserve** and structural polysaccharides,
 - and **type of life** history
- reflect the **varied evolutionary origins of this heterogeneous assemblage of organisms, including both prokaryote and eukaryote species.**



- The term algae refers to both macroalgae and a highly diversified group of microorganisms known as microalgae.
- The number of algal species has been estimated to be one to ten million, and most of them are microalgae.

Algae do not have any of these features;

- They do not have roots, stems, leaves, nor well-defined vascular tissues. Even though many seaweeds are plant-like in appearance and some of them show specialization and differentiation of their vegetative cells,
- They do not form embryos,
- Their reproductive structures consist of cells that are potentially fertile and lack sterile cells covering or protecting them.
- Parenchymatous development is present only in some groups
- Have both monogenetic and digenetic life cycles.
- Moreover, algae occur in dissimilar forms such as microscopic single cell, macroscopic multicellular loose or filmy conglomerations, matted or branched colonies, or more complex leafy or blade forms, which contrast strongly with uniformity in vascular plants.



WHY THE INTEREST IN THE ALGAE?

Why are algae important?

Why is there so much current interest in the algae?

- Algae, for practical purposes, are the only primary producers in the oceans—an area that covers 71% of the Earth's surface. Microscopic algae and seaweeds directly or indirectly **support most life in the seas**. Indeed, there are approximately 6.25×10^{25} algal cells in the oceans at any one time. And, assuming an average diameter of 2 μm , these cells could be packed into a plank-sized volume with dimensions 7 cm thick, 30 cm wide, and long enough to extend from the earth to the moon (386,000 km)! Assuming that the cells divide once per day, the oceans produce another plank each day. Unlike the terrestrial environment, where biomass accumulates, the consumers of our oceans eat one plank each day. Therefore, while algae may seem insignificant in terms of accumulated biomass, they are very significant in terms of global productivity.

WHY THE INTEREST IN THE ALGAE?

Why are algae important?

Why is there so much current interest in the algae?

- They are crucial to the functioning of the planet. They are **oxygen producers**; they dominate the world's oceans and account for the production of a major fraction of the world's oxygen. They contribute approximately 40 to 50% of the oxygen in the atmosphere, or the oxygen in every other breath we breathe.
- Algae are the original source of fossil carbon found in crude oil and natural gas.

WHY THE INTEREST IN THE ALGAE?

Why are algae important?

Why is there so much current interest in the algae?

- Algae are also important economically.
 - Seaweed sales account for approximately 22% of the 9.4 million metric tons of aquaculture products sold worldwide.
 - A lot of products are also derived from the algae, including alginates and carrageenans and agar that are employed in a wide range of industrial products e.g. gelling agents, toothpastes, cosmetics, paper sizing, emulsifiers, and bandages; in almost all walks of life it is likely that some algal product will be involved.
- Some algae can also be a nuisance. Through fish kills, the intoxication of shellfish, and unsightly water discolorations, "harmful algal blooms" (HABs) have received growing and worldwide attention.

WHY THE INTEREST IN THE ALGAE?

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Why is there so much current interest in the algae?

- They are a major source of food for plankton, fisheries, and, via the food chain, ultimately for humans.
- Some species are the basis of the structure of the ecosystem, for example, the giant kelp forests.
- Many algae are eaten directly as food in different parts of the world, e.g. nori (the wrapping of *Porphyra* around sushi) in Japan.

- A **eukaryotic cell** (Fig. 1.1) is often surrounded by a cell wall composed of polysaccharides that are partially produced and secreted by the Golgi body.
- The plasma membrane (plasmalemma) surrounds the remaining part of the cell; this membrane is a living structure responsible for controlling the influx and outflow of substances in the protoplasm.
- Locomotory organs, the flagella, propel the cell through the medium by their beating. The flagella are enclosed in the plasma membrane and have a specific number and orientation of microtubules.

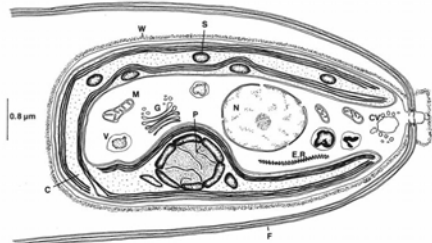


Fig. 1.1 Drawing of a cell of the green alga *Chlamydomonas* showing the organelles present in a eukaryotic algal cell. (C) Chloroplast; (CV) contractile vacuole; (E.R.) endoplasmic reticulum; (F) flagella; (G) Golgi body; (M) mitochondrion; (N) nucleus; (P) pyrenoid; (S) starch; (V) vacuole; (W) wall.

Structure of the algal cell

- There are two basic types of cells in the algae, **prokaryotic** and **eukaryotic**.
- Prokaryotic cells lack membrane-bounded organelles (plastids, mitochondria, nuclei, Golgi bodies, and flagella) and occur in the **cyanobacteria** (Fig. 2.11). The remainder of the algae are eukaryotic and have organelles.

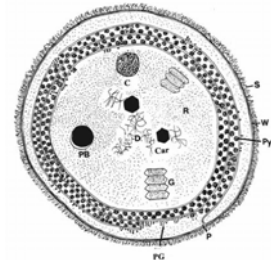


Fig. 2.11 Drawing of the fine-structural features of a cyanobacterial cell. (C) Cyanophycin body structured granule; (Car) carboxysome (polyhedral body); (D) DNA fibrils; (G) gas vesicles; (P) plasmalemma; (PB) polyphosphate body; (PG) polyglucan granules; (Py) phycobilisomes; (R) ribosomes; (S) sheath; (W) wall.

- Double-membrane-bounded **mitochondria** have 70S ribosomes and DNA, and contain the respiratory apparatus.
- The **Golgi body** consists of a number of membrane sacs, called cisternae, stacked on top of one another. The Golgi body functions in the production and secretion of polysaccharides.
- The cytoplasm also contains large 80S ribosomes and lipid bodies.

- The **nucleus**,
 - contains the genetic material of the cell, surrounded by a double membrane with pores in it.
 - The contents of the nucleus are a nucleolus, chromosomes, and the background material or karyolymph.
- The **chloroplasts**
 - have membrane sacs called **thylakoids** that carry out the light reactions of photosynthesis.
 - The thylakoids are embedded in the **stroma** where the dark reactions of carbon fixation take place.
 - The stroma has small **70S ribosomes, DNA**, and in some cases the **storage product**.
 - Chloroplasts are surrounded by the two membranes of the **chloroplast envelope**.
 - Sometimes chloroplasts have a dense proteinaceous area, the **pyrenoid**, which is associated with storage-product formation.

- A flagellum consists of an **axoneme** of nine doublet microtubules that surround two central microtubules, with all of the microtubules encased in the plasma membrane (Figs. 1.2, 1.3).

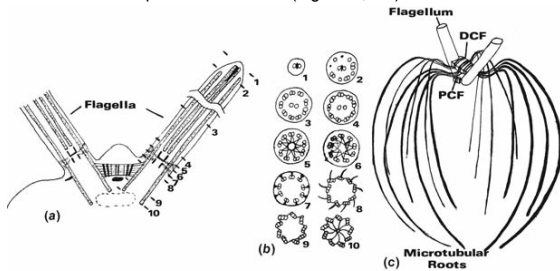
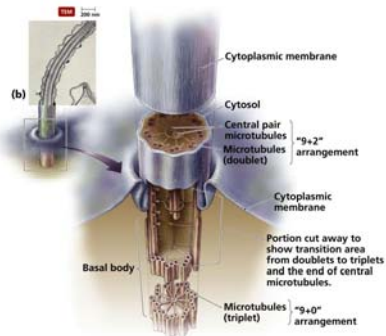


Fig. 1.2 The flagellar system in the green alga *Chlamydomonas*. (a) A diagrammatic drawing of a section of the flagellar system. The numbers refer to cross sections of the flagellar system in (b). (c) Diagrammatic drawing of the whole flagellar apparatus. The two flagella are joined by the proximal connecting fiber (PCF) and distal connecting fiber (DCF). (After Ringo, 1967.)

Flagella

- Flagella can be defined as motile cylindrical appendages found in widely divergent cell types throughout the plant and animal kingdom, which either move the cell through its environment or move the environment relative to the cell.
- The flagella of the green alga *Chlamydomonas* have been used as a model of flagellar structure.
- Flagella structure has been highly conserved throughout evolution, images from *Chlamydomonas* are virtually **indistinguishable** from flagella (or cilia – a term for a short flagellum) of mammalian cells including human sperm and certain epithelia.
- *Chlamydomonas* has been chosen because of the ease of growing the organism and because the flagella can be detached from the cells by pH shock or blending.
- Since the flagella are not essential for viability of the cell, it is relatively easy to isolate mutations affecting flagella synthesis by the cells.

- On entering the cell body, the two central microtubules end at a dense plate, whereas the nine peripheral doublets continue into the cell, usually picking up an additional structure that transforms them into triplets.
- The flagellum passes through a tunnel in the cell wall called the **flagellar collar**.



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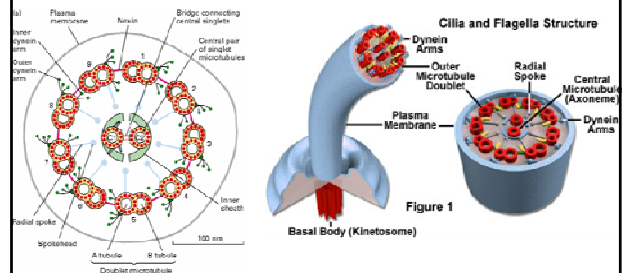


Figure 1

- The central pair of microtubules are single microtubules with 13 protofilaments while the outer microtubules are doublets with the A-tubule consisting of 13 protofilaments and the B-tubule having 11 protofilaments.
- The central pair microtubules resemble cytoplasmic microtubules, in that they are more labile than the outer doublet microtubules.
- The axoneme microtubules are composed of α - and β -tubulin which make up 70% of the protein mass of the axoneme.
- Radial spokes**, each consisting of a thin stalk and head, project from the A-tubule of the outer microtubule doublets (Figs. 1.2, 1.3).

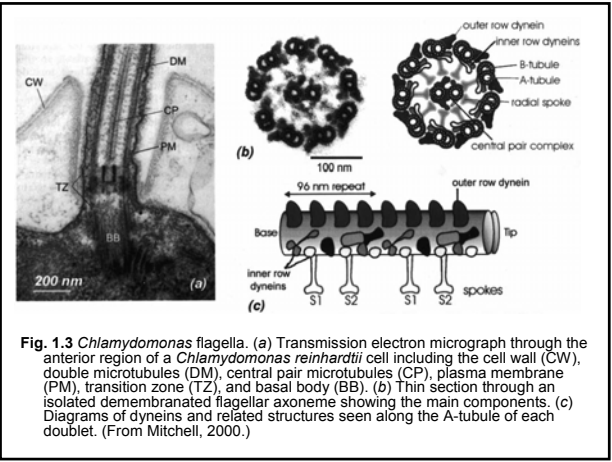
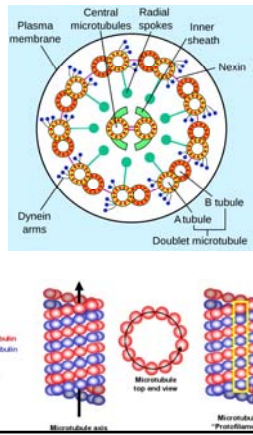
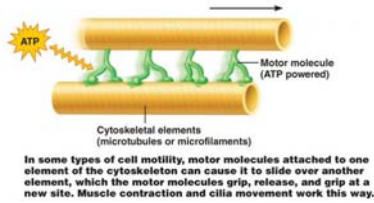
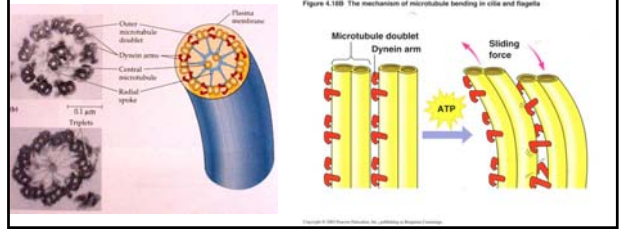


Fig. 1.3 *Chlamydomonas* flagella. (a) Transmission electron micrograph through the anterior region of a *Chlamydomonas reinhardtii* cell including the cell wall (CW), double microtubules (DM), central pair microtubules (CP), plasma membrane (PM), transition zone (TZ), and basal body (BB). (b) Thin section through an isolated demembrated flagellar axoneme showing the main components. (c) Diagrams of dyneins and related structures seen along the A-tubule of each doublet. (From Mitchell, 2000.)



- Inner and outer **dynein arms** attach to the A-tubule of the outer microtubule doublet and extend to the B-tubule of the adjacent outer microtubule doublet.
- Dynein is a mechanoenzyme (also called molecular motor or motor molecule) that hydrolyzes ATP with the resulting energy used by dynein to move along the B-tubule of the adjacent outer microtubule doublet (Fig. 1.3).
- In this action, the B-tubule is called the **track** while the A-tubule is called the **cargo**.
- The resulting displacement of outer microtubule doublets in relation to each other causes bending of the flagellum.



- There are also other structures between the microtubules in the basal region of the flagellum (**basal body**). Attached to the basal body there can be either **microtubular roots** or **striated fibrillar roots**.
- The former type of root consists of a group of microtubules running from the basal body into the protoplasm (Figs. 1.2, 1.5), whereas the latter consists of groups of fibers that have striations along their length (Figs. 1.5, 1.6)
- The gamete of the green seaweed *Ulva lactuca* (sea lettuce) has both types of flagellar roots (Fig. 1.5).

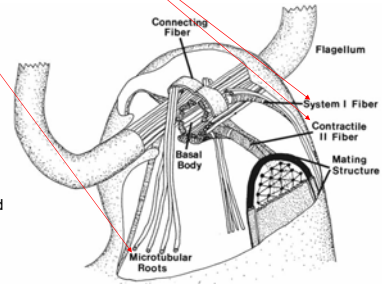


Fig. 1.5 Schematic three-dimensional reconstruction of the flagellar apparatus of a female gamete of *Ulva lactuca* showing the four cruciately arranged microtubular roots and the fibrous contractile roots. (Adapted from Melkonian, 1980.)

- Kinesin proteins (like dynein also belonging to motor proteins) cause the central pair of microtubules to rotate within the axoneme (Fig. 1.4).
- As the central pair of microtubules rotates, the microtubules interact with the individual radial spokes inducing sliding between adjacent microtubule doublets, asymmetric bending of the flagellum and propagation of flagellar waves.

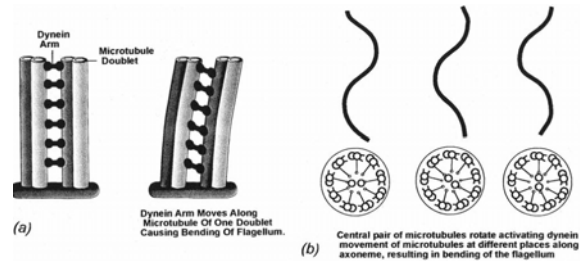


Fig. 1.4 Bending of flagella occurs by the rotating central pair of microtubules activating dynein movement of specific outer doublet microtubules.

- There are four **microtubular roots** composed of microtubules arranged in a cruciate pattern, and **fibrous roots (rhizoplasts)** composed of a bundle of filaments (Fig. 1.5, 1.6).
- There are two types of fibrous roots (Fig. 1.5):
 - (1) **system I fibrous roots** composed of 2 nm filaments cross-striated with a periodicity of approximately 30 nm and
 - (2) **system II fibrous roots** composed of 4–8 nm filaments usually crossstriated with a periodicity greater than 80 nm.
- System I fibrous roots are non-contractile while system II fibrous roots are contractile when appropriately stimulated.

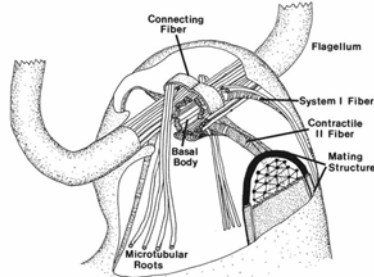


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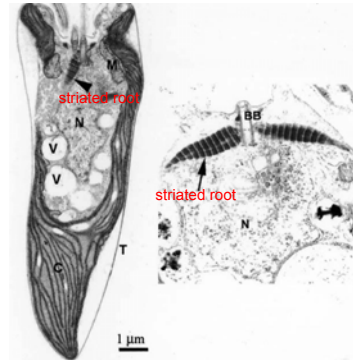


Fig. 1.6 Transmission electron micrographs of striated roots (rhizoplasts) in the green alga *Scherffelia dubia* (Chlorophyta). Arrow and arrowhead point to a striated root. (BB) Basal body; (C) chloroplast; (M) mitochondrion; (N) nucleus; (V) vacuole.

- There are **two types of flagellar hair** (Fig. 1.7):
- **1 Non-tubular flagellar hairs** made up of solid fibrils 5–10 nm wide and 1–3 µm long that are composed of glycoproteins. These hairs are flexible and wrap around the flagellum increasing the surface area and efficiency of propulsion.
- **2 Tubular flagellar hairs** about 2 µm long composed of three regions:
 - (1) a tapering basal region 200 nm long attached to the flagellar membrane,
 - (2) a microtubular shaft 1 µm long, and
 - (3) a few 0.52 µm-long terminal filaments.

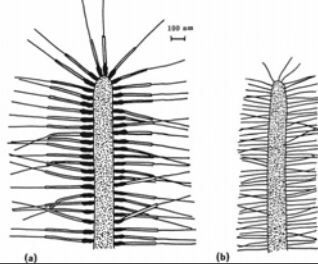
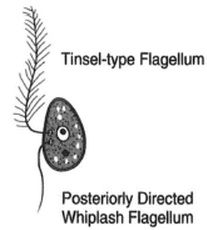


Fig. 1.7 Drawings of the types of hairs on algal flagella. (a) Tripartite hairs (example *Ascophyllum sperm*). Each hair is composed of a basal region attached to the flagellar membrane, the microtubular shaft, and a terminal hair. (b) Non-tubular hairs (example *Chlamydomonas* gamete).

- The flagellar membrane may
 - have **no hairs (mastigonemes)** on its surface (**whiplash or acronematic flagellum**)
 - or it may have hairs on its surface (**tinsel or hairy or pantonematic or Flimmergeißel**).



•Flagella progress through a set of developmental cycles during cell division (Fig. 1.8).

- A biflagellate cell with an anterior flagellum covered with tubular hairs (tinsel flagellum), and a posterior smooth flagellum (whiplash flagellum), will be used as an example.
- Before the onset of cell division, **two new flagella appear** next to the anterior flagellum.
- These two new flagella elongate while the **original anterior flagellum** moves toward the posterior of the cell and loses its tubular hairs, to become the posterior smooth flagellum of one of the daughter cells.
- The two new flagella at the anterior end of the cell acquire tubular hairs and become the tinsel flagella of the daughter cells.
- Thus, each daughter cell has one new anterior tinsel flagellum, and one posterior smooth whiplash flagellum that was originally a flagellum in the parent cell.

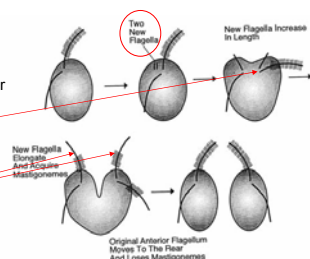


Fig. 1.8 The sequence of flagellar transformation during cell division

- The bases of the hairs do not penetrate the flagellar membrane but are stuck to it.
- **Development** of the tubular hairs
 - begins in the space between the inner and outer membrane of the nuclear envelope (peri nuclear continuum) where the basal and microtubular regions are assembled.
 - These then pass to the Golgi apparatus, where the terminal filaments are added.
 - Finally the hairs are carried to the plasma membrane in Golgi vesicles, where they are discharged and attached to the flagellar membrane.
- **Tripartite tubular hairs** occur in the Heterokontophyta.
- The term **stramenopile** (straw hair) has been used to include **all protists** with tubular hairs.
- The remainder of the algae have non-tubular hairs if hairs occur on the flagella.
- In addition to hairs, a number of different **scale** types occur on the surface of the flagella.

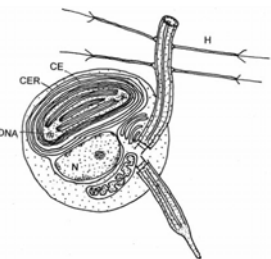


Fig. 16.1 Semi-diagrammatic drawing of the cytology of *Bolidomonas*. Heterokontophyta (CE) Chloroplast envelope; (CER) chloroplast endoplasmic reticulum; (H) tripartite flagellar hair; (N) nucleus.

- Motile algal cells are typically **biflagellate**, although **quadriflagellate** types are commonly found in green algae.
- A **triflagellate** (type of zoospore) and the **uniflagellate** (few) forms are also found.
- Intermediate cases exist, which carry a short second flagellum, where it is reduced to a stub in some species, or reduced to a nonfunctional basal body attached to the functional one in other species.
- A special case of multiflagellate alga where the numerous flagella form a ring or crown around the apical portion of the cell (**stephanokont**).

- Algal cells can have different **arrangements of flagella** (Fig. 1.9).
 - If the flagella are of equal length, they are called **isokont** flagella;
 - if they are of unequal length, they are called **anisokont flagella**; and
 - if they form a ring at one end of the cell, they are called **stephanokont** flagella.
- **Heterokont** refers to an organism with a hairy and a smooth flagellum.

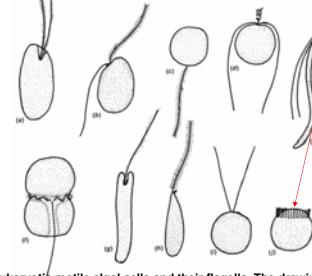
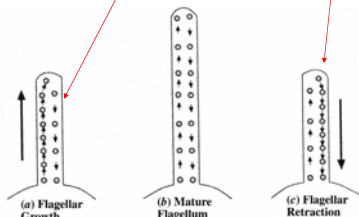


Fig. 1.9 The shape of eukaryotic motile algal cells and their flagella. The drawings represent the common arrangement of flagella in the groups. There are a number of modifications in structure that are not included here. (a) Cryptophyta; (b) most of the Heterokontophyta; (c) Bacillariophyceae of the Heterokontophyta; (d) Prymnesiophyta; (e) Chlorophyta; (f) Dinophyta; (g) Euglenophyta; (h) Eustigmatophyceae of the Heterokontophyta; (i, j) Chlorophyta.

- A change in length of the flagellum is produced by an imbalance in the assembly or disassembly of flagellar components.
- Thus, disassembly occurs faster than assembly in **flagellar retraction**.
- The opposite occurs during **flagellar growth**.
- The differences in length of flagella arise from the shorter flagellum being **delayed** in the initial stages of construction.
- The assembly **rate** of the shorter flagellum is the same as the longer flagellum.
- There may be a **gate** at the base of the flagellum that regulates the passage of flagellar precursors into the basal body and the flagellum.



- **Flagella can be of different length in the same cell.** This is controlled by **intraflagellar transport**, defined as the **bi-directional movement of particles along the length of the flagellum between the axoneme and the flagellar membrane**.
- A **mature flagellum** that is not elongating has a steady disassembly of the flagellum that is countered by an equally steady assembly provided by intraflagellar transport (Fig. 1.10).

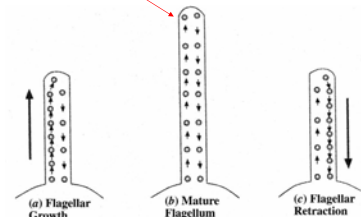


Fig. 1.10 (a) Intraflagellar transport results in more assembly of flagellar subunits than disassembly during flagellar growth. (b) A mature flagellum has an equal amount of assembly and disassembly of flagellar subunits. (c) There is more disassembly of flagellar subunits during flagellar retraction.

- The **amorphous mucilaginous** components occur in the greatest amounts in the Phaeophyceae and Rhodophyta, the polysaccharides of which are commercially exploited.
- **Alginic acid** (Fig. 1.11) is a polymer composed mostly of β -1,4 linked D-mannuronic acid residues with variable amounts of L-guluronic acid. Alginic acid is present in the intercellular spaces and cell walls of the Phaeophyceae.
- **Fucoidin** (Fig. 1.11) also occurs in the Phaeophyceae and is a polymer of α -1, 2, α -1, 3, and α -1, 4 linked residues of L-fucose sulfated at C-4.
- **Galactans** In the Rhodophyta the amorphous component of the wall is composed of galactans or polymers of galactose, which are alternatively β -1,3 and β -1,4 linked. These galactans include **agar** (made up of **agarpectin** and **agarose**, Fig. 1.11) and **carrageenan** (Fig. 4.15).

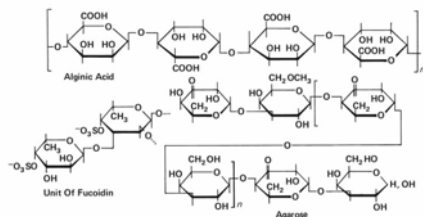


Fig. 1.11 Structural units of alginic acid, fucoidin, and agarose.

Cell walls and mucilages

In general, algal cell walls are made up of two components:

- (1) the **fibrillar component**, which forms the skeleton of the wall, and
- (2) the **amorphous component**, which forms a matrix within which the fibrillar component is embedded.

- The most common type of **fibrillar component** is **cellulose**, a polymer of 1,4 linked β -D-glucose.
- Cellulose is replaced by a **mannan**, a polymer of 1,4 linked β -D-mannose, in some siphonaceous greens, and in *Porphyra* and *Bangia* in the Rhodophyta.
- In some siphonaceous green algae and some Rhodophyta (*Porphyra*, *Rhodochorton*, *Laurencia*, and *Rhodomenia*), fibrillar **xylans** of different polymers occur.

Plastids

- The basic type of plastid in the algae is a **chloroplast**, a plastid capable of photosynthesis.
- Chromoplast** is synonymous with chloroplast; in the older literature a chloroplast that has a color other than green is often called a chromoplast.
- A **proplastid** is a reduced plastid with few if any thylakoids. A proplastid will usually develop into a chloroplast although in some heterotrophic algae it remains a proplastid.
- A **leucoplast** or **amyloplast** is a colorless plastid that has become adapted for the accumulation of storage product.

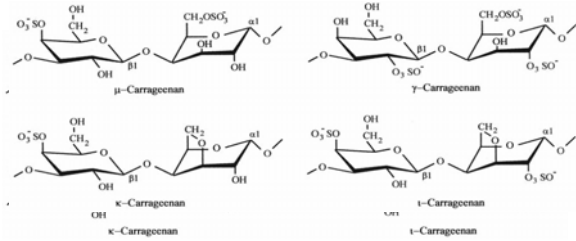
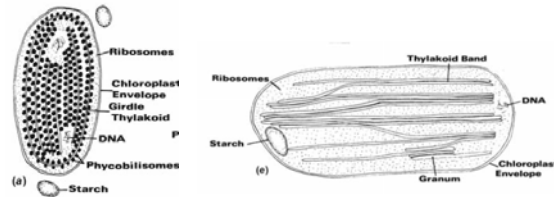


Fig. 4.15 The chemical structures of the different types of carrageenans that occur in the red algae.

- In the other eukaryotic algae, the chloroplast envelope is surrounded by **one** or **two** membranes of **chloroplast endoplasmic reticulum** (chloroplast E.R.), which has ribosomes attached to the outer face of the membrane adjacent to the cytoplasm.
- The chloroplast E.R. is the remnant of the food vacuole membrane and/or the plasma membrane involved in the original endosymbiosis leading to the chloroplasts in a secondary endosymbiosis.

- In the Rhodophyta and Chlorophyta, the chloroplasts are bounded by the double membrane of the chloroplast envelope (Fig. 1.12(a), (e)).

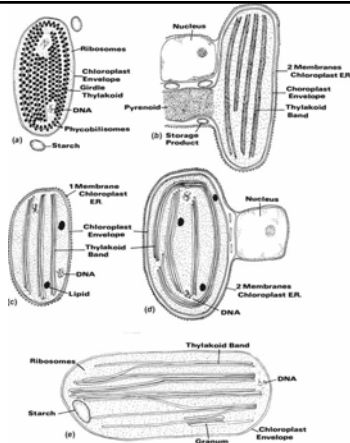


(a) One thylakoid per band, no chloroplast endoplasmic reticulum (Rhodophyta).

(e) Two to six thylakoids per band, no chloroplast E.R. (Chlorophyta).

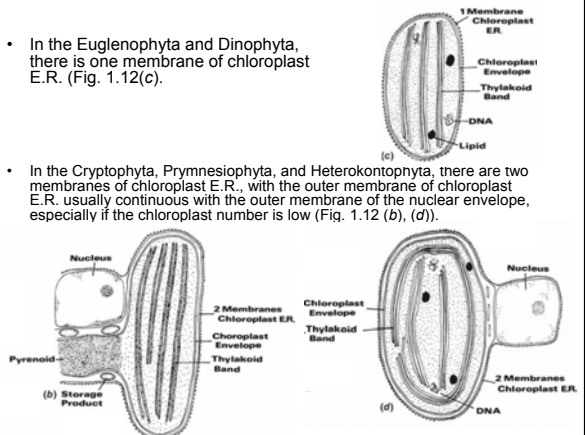
Fig. 1.12 Types of chloroplast structure in eukaryotic algae.

- (a) One thylakoid per band, no chloroplast endoplasmic reticulum (Rhodophyta). (b) Two thylakoids per band, two membranes of chloroplast E.R. (Cryptophyta). (c) Three thylakoids per band, one membrane of chloroplast E.R. (Dinophyta, Euglenophyta). (d) Three thylakoids per band, two membranes of chloroplast E.R. (Prymnesiophyta and Heterokontophyta). (e) Two to six thylakoids per band, no chloroplast E.R. (Chlorophyta).

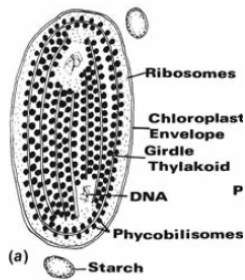
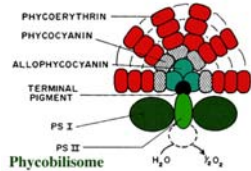


- In the Euglenophyta and Dinophyta, there is one membrane of chloroplast E.R. (Fig. 1.12(c)).

- In the Cryptophyta, Prymnesiophyta, and Heterokontophyta, there are two membranes of chloroplast E.R., with the outer membrane of chloroplast E.R. usually continuous with the outer membrane of the nuclear envelope, especially if the chloroplast number is low (Fig. 1.12 (b), (d)).

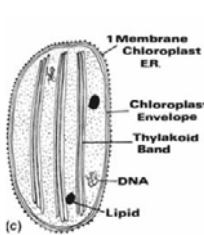


- In the cyanobacteria and Rhodophyta (Fig. 1.12(a)), the thylakoids are usually free from one another, with **phycobilisomes** (containing the phycobiliproteins) on the surface of the thylakoids.
- The phycobilisomes on the surface of one thylakoid alternate with those on the surface of an adjacent thylakoid.
- The phycobilisomes appear as 35-nm granules when phycoerythrin predominates, or as discs when phycocyanin predominates.

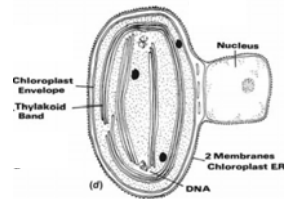


- The basic structure of the photosynthetic apparatus in a plastid consists of a series of flattened membranous vesicles called **thylakoids** or **discs**, and a surrounding matrix or **stroma**.
- The thylakoids contain the chlorophylls and are the sites of the photochemical reactions; carbon dioxide fixation occurs in the stroma. The thylakoids can be free from one another or grouped to form **thylakoid bands**.

- In the Euglenophyta and Heterokontophyta the thylakoids are grouped in bands of three with a girdle or peripheral band running parallel to the chloroplast envelope.
- In the Dinophyta, Prymnesiophyta, and Eustigmatophyceae, the thylakoids are also in bands of three, but there is no girdle band (Fig.1.12(c), (d)).

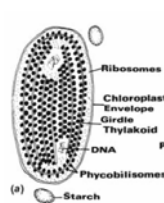


(c) Three thylakoids per band, one membrane of chloroplast E.R. (Dinophyta, Euglenophyta).

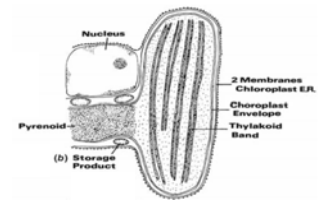


(d) Three thylakoids per band, two membranes of chloroplast E.R. (Prymnesiophyta and Heterokontophyta).

- In the more primitive members of the Rhodophyta the thylakoids terminate close to the chloroplast envelope, whereas in advanced members of the Rhodophyta peripheral thylakoids are present, which enclose the rest of the thylakoids.
- In the Cryptophyta, the chloroplasts contain bands of two thylakoids (Fig.1.12(b)); the phycobiliproteins are dispersed within the thylakoids.

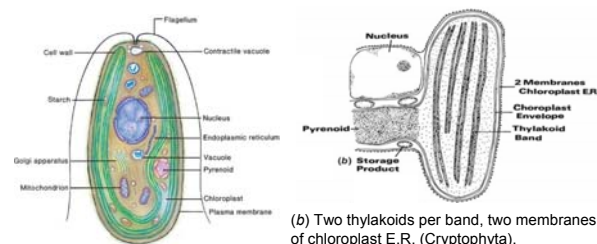


Rhodophyta



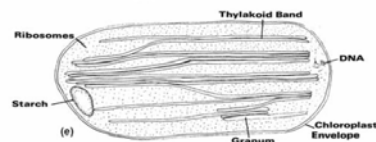
(b) Two thylakoids per band, two membranes of chloroplast E.R. (Cryptophyta).

- A **pyrenoid** (Fig. 1.12(b)) is a differentiated region within the chloroplast that is denser than the surrounding stroma and may or may not be traversed by thylakoids.
- A pyrenoid is frequently associated with storage product.
- Pyrenoids contain ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco), the enzyme that fixes carbon dioxide.
- Consequently, the size of the pyrenoid will vary depending on how much Rubisco is present.



(b) Two thylakoids per band, two membranes of chloroplast E.R. (Cryptophyta).

- In the Chlorophyta, the thylakoids occur in bands of two to six, with thylakoids running from one band to the next.



(e) Two to six thylakoids per band, no chloroplast E.R. (Chlorophyta).

- The above grouping of algal thylakoids into bands occurs under **normal growth conditions**. Abnormal growth conditions commonly cause lumping of thylakoids and other variations in structure.

- The common ancestor of all ribulose-1,5-bisphosphate carboxylase was probably similar to Form II and was adapted to the anaerobic conditions and high CO₂ concentrations prevailing in the ancient earth.
- Form I evolved as the earth's atmosphere became oxygenated, and CO₂ concentration declined and with it the need for a greater affinity for CO₂.
- The greater affinity for CO₂ in Form I, however, came at the price of reduced catalytic efficiency.

- Rubisco exists in two forms :
- 1 Form I** occurs in some bacteria, the cyanobacteria, in all green plants and nongreen plants. Form I is composed of eight large subunits and eight small subunits (Fig. 1.13).

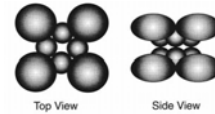


Fig. 1.13 The structure of Form I variation of Rubisco showing the eight large subunits and eight small subunits.

- Form I has a high affinity for CO₂ and a low catalytic efficiency (low rate of CO₂ fixation).
- In green algae, euglenoids, and green plants, the large subunit is coded by chloroplast DNA and the small subunit by nuclear DNA.
- In the cyanelle (endosymbiotic cyanobacterium) of *Cyanophora paradoxa* and in some non-green algae, both subunits are coded by chloroplast DNA.
- 2 Form II** occurs in some eubacteria and in the dinoflagellates and is composed of two large subunits. Form II has a low affinity for CO₂ and a high catalytic efficiency.

Visual systems

- The essential elements of the visual systems are the **eyespot** and the detector, that is, the true **photoreceptor(s)**. When the eyespot is absent its function is performed by the whole algal body.
- Many motile algae have groups of tightly packed carotenoid lipid-globules that constitute an orange-red **eyespot or stigma** (Fig. 5.2) that is involved in response to light.

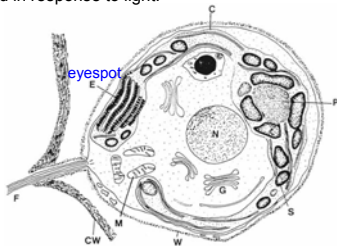
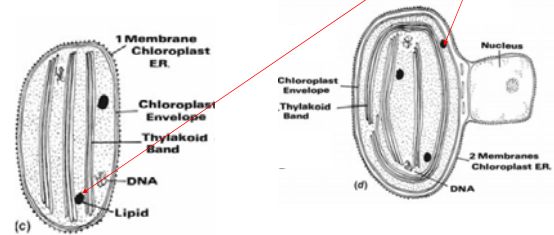


Fig. 5.2 Semi-diagrammatic drawing of a cell in a *Volvox* vegetative colony. The colony wall (CW) is distinct from the cell wall (W). (C) Chloroplast; (E) eyespot; (F) flagellum; (G) Golgi; (M) mitochondrion; (N) nucleus; (P) pyrenoid; (S) starch.

- Chloroplasts contain small (30–100 nm), spherical **lipid droplets** between the thylakoids (Fig.1.12 (c), (d)). These lipid droplets serve as a pool of lipid reserve within the chloroplast.



(c) Three thylakoids per band, one membrane of chloroplast E.R. (Dinophyta, Euglenophyta).

(d) Three thylakoids per band, two membranes of chloroplast E.R. (Prymnesiophyta and Heterokontophyta).

- The eyespot has a different structure in the different groups of algae.
- Eyespots have certain basic characteristics:
 - (1) Eyespots usually have carotenoid-rich lipid globules packed in a highly ordered hexagonal arrangement.
 - (2) Eyespots are usually single structures in peripheral positions, most often oriented perpendicular to the axis of the swimming path.

Very often the photoreceptor cannot be identified by optical microscopy, while the eyespot can be seen easily because of its size and color, usually orange-red.

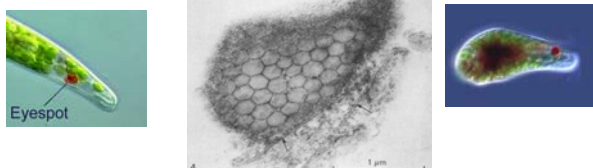


Fig. . Tangential section through the eyespot area of female gamete. Hexagonal arrangement of eyespot lipid globules is seen. Arrows, microtubules approaching the eyespot area.

- The most common type of photoreceptor consists of extensive two-dimensional patches of photosensitive proteins, present in the plasma membrane in close association with the eyespot.
- The **photoreceptor** in the green alga *Chlamydomonas* is **chlamyrodopsin** (Fig. 1.15) in the plasma membrane over the eyespot.

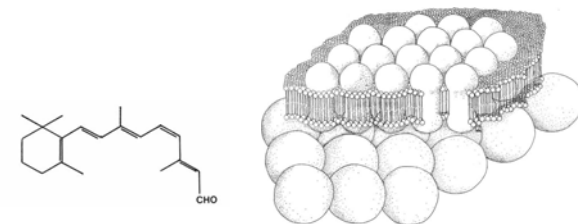
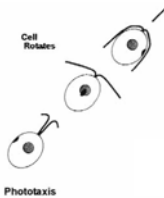


Fig. 1.15 The structure of chlamyrodopsin, the photoreceptor in *Chlamydomonas*.

Schematic drawing of photoreceptor system.

- Phototaxis in *Chlamydomonas* is controlled by the beating of each flagellum. The flagellum closest to the eyespot is the **cis** flagellum while the **trans** flagellum is furthest from the eyespot.
- The light is received by the photoreceptor which controls the opening and closing of calcium channels, and the level of intraflagellar calcium concentration.
- The calcium concentration within the flagellum effects the interactions of the radial spokes with the central pair of microtubules.
- When the plasma membrane of *Chlamydomonas* is made permeable, *Chlamydomonas* cells swim normally at 10^{-8} M calcium in the medium.
- Decreasing the calcium to 10^{-9} M reduces the stroke velocity of the trans flagellum, while increasing the calcium to 10^{-7} M reduces the stroke velocity of the cis flagellum.



- Motile algae exhibit three types of responses to light (Fig. 1.14):
 - phototaxis, photophobia and gliding.
- **1 Phototaxis.** In phototaxis, the orientation of cell movement is affected by the **direction and intensity of light**.
- The cells move toward the light in **positive phototaxis** and away from the light in **negative phototaxis**.

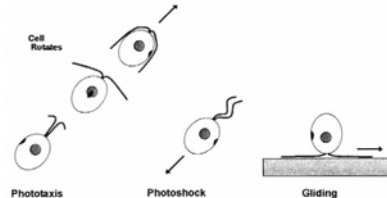
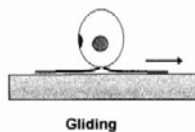


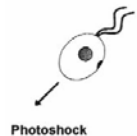
Fig. 1.14 Three types of flagellar orientation in *Chlamydomonas*. In **phototaxis**, the cells swim forward and rotate. Phototaxis requires that cells swim forward in a spiral path that causes rotation of the symmetrically placed eyespot. In **photoshock**, the cell has a transient avoidance response that causes the cell to swim backwards. In **gliding**, the leading flagellum and passive flagellum are 180° apart.

- **3 Gliding (quiescence).** In gliding, the flagella stop beating and adhere to a surface or an air/water interface.
- The cells can glide over the surface with one flagellum actively leading and the other passively trailing (Fig. 1.14).



- Cells may switch direction by changing which flagellum is active.
- Gliding motility may be a common phenomenon among organisms that live in the thin film of water on soil particles.

- **2 Photophobia (photoshock).** Photophobia is a change in direction of movement of the cell **caused by a rapid change in light intensity, irrespective of the direction of the light**.
- Swimming cells stop and change the beat pattern from the normal asymmetric flagellar stroke to a symmetrical stroke that propels the cell backward (Fig. 1.14).
- At the end of the photophobic response, the cells tumble and resume swimming in a new direction.
- Laboratory experiments with *Chlamydomonas* link photophobic responses to increases in calcium above 10^{-6} M.
- Unlike phototaxis, interactions between radial spokes and central-pair microtubules are not necessary for a photophobic reaction.



- **Most chloroplasts contain prokaryotic DNA** in an area of the chloroplast devoid of 70S ribosomes (Figs. 1.16 and 1.17).
- The DNA is an evolutionary remnant of the cyanobacterium involved in the endosymbiosis leading to the chloroplast.
- The individual DNA microfibrils are circular, are attached to the chloroplast membranes, and lack basic proteins (**histones**).

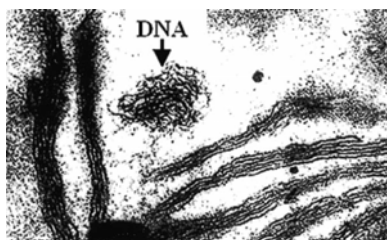
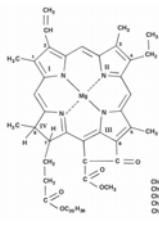


Fig. 1.16 Transmission electron micrograph of DNA in the chloroplast of the dinoflagellate *Prorocentrum micans*.

- In the Chlorophyta, Cryptophyta and most of the Heterokontophyta, the eyespot occurs as lipid droplets in the chloroplast.
- In the Euglenophyta, Eustigmatophyceae, and Dinophyta, the eyespot occurs as a group of membrane-bounded lipid droplets, free of the chloroplast.

- The photosynthetic algae have chlorophyll in their chloroplasts.
- **Chlorophyll** is composed of a porphyrin-ring system that is very similar to that of hemoglobin but has a magnesium atom instead of an iron atom (Fig. 1.18).
- The algae have four types of chlorophyll, a, b, c (c1 and c2), and d.
- Chlorophyll a is the primary photosynthetic pigment (the light receptor in photosystem I of the light reaction) in all photosynthetic algae and ranges from 0.3% to 3.0% of the dry weight.
- Chlorophyll a is insoluble in water and petroleum ether but soluble in alcohol, diethyl ether, benzene, and acetone.
- The pigment has two main absorption bands in vitro, one band in the red light region at 663 nm and the other at 430 nm (Fig. 1.19).



Chl a: as shown in structure
 Chl b: -CH₃ = CH₂
 Chl c: -CH₃ = CH₂
 Chl c₁: -CH₃ = CH₂OH; double bond at IV-7, 8
 Chl c₂: -CH₃ = CH₂OH; double bond at IV-7, 8
 Chl d: -CH₃ = CH₂OH; double bond at IV-7, 8
 R = C₃₅H₇₁

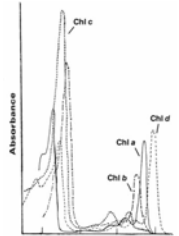


Fig. 1.19 The absorption spectra of chlorophylls a, b, c, and d.

Fig. 1.18 The structure of the chlorophylls.

- The algae can be divided into **two general groups** according to the distribution of DNA in the plastids.

- In the **first group**, the clumps of DNA (**nucleoids**) are scattered through out the plastids. This group includes the Cryptophyta, Dinophyta, Prymnesiophyta, Eustigmatophyceae, Rhodophyta, and Chlorophyta.
- In the **second group**, the DNA occurs in a ring just within the girdle lamella. This group includes the Chrysophyceae, Bacillariophyceae, Raphidophyceae, and Xanthophyceae (with the exception of *Vaucheria* and three genera known to lack girdle lamellae – *Bumilleria*, *Bumilleriopsis*, and *Pseudobumilleriopsis*).
- The Euglenophyta fit into neither group, showing a variable distribution of chloroplast DNA.

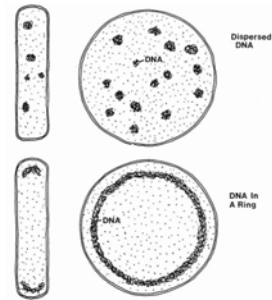


Fig. 1.17 Semidiagrammatic drawing of the two types of distribution of DNA in algal chloroplasts. Side and face views of the plastids are drawn.

- **Chlorophyll c** (Fig. 1.18) is found in the Dinophyta, Cryptophyta, and most of the Heterokontophyta.
- Chlorophyll c has two spectrally different components: chlorophyll c₁ and c₂.
- Chlorophyll c₂ is always present, but chlorophyll c₁ is absent in the Dinophyta and Cryptophyta.
- The ratio of chlorophyll a to chlorophyll c ranges from 1.2:2 to 5.5:1.
- Chlorophyll c probably functions as an accessory pigment to photosystem II.
- The pigment is soluble in ether, acetone, methanol, and ethyl acetate, but is insoluble in water and petroleum ether.
- Extracted chlorophyll c₁ has main absorption maxima at 634, 583, and 440 nm in methanol, whereas chlorophyll c₂ has maxima at 635, 586, and 452 nm.

- Whereas chlorophyll a is found in all photosynthetic algae, the **other algal chlorophylls** have a more limited distribution and function as accessory photosynthetic pigments.
- **Chlorophyll b** is found in the Euglenophyta and Chlorophyta (Fig. 1.18). Chlorophyll b functions photosynthetically as a light-harvesting pigment transferring absorbed light energy to chlorophyll a.
- The ratio of chlorophyll a to chlorophyll b varies from 2:1 to 3:1.
- The solubility characteristics of chlorophyll a are similar to chlorophyll b, and in vitro chlorophyll b has two main absorption maxima in acetone or methanol, one at 645 nm and the other at 435 nm (Fig. 1.19).

- The light-harvesting complexes use different antennae pigment complexes to capture light energy.
- All of the light-harvesting complexes are composed of three-membrane spanning helices (Fig. 1.20).

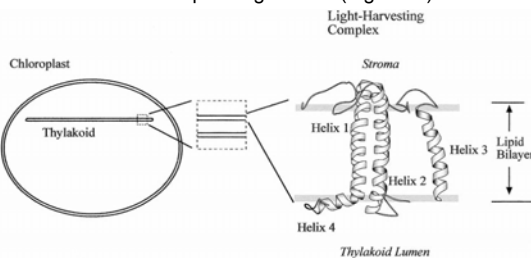
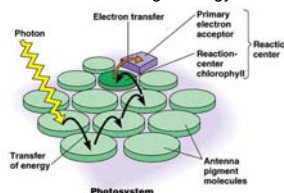


Fig. 1.20 The basic structure of the light-harvesting complex in all eukaryotic plants. Three transmembrane helices traverse the membrane. The similarity of the light harvesting complex in all eukaryotic plants is an argument for the chloroplast arising from a single endosymbiotic event.

- **Chlorophyll d** (Fig. 1.18) occurs in some cyanobacteria.
- It has three main absorption bands at 696, 456, and 400 nm.
- The photosynthetically active pigments of algae are gathered in discrete pigment-protein complexes which can be divided functionally into two groups :
 - **1 the photochemical reaction center** containing chlorophyll a, where light energy is converted into chemical energy;
 - **2 the light-harvesting complexes** that serve as antennae to collect and transfer available light energy to the reaction center.



- **Carotenoids** are yellow, orange, or red pigments that usually occur inside the plastid but may be outside in certain cases. In general, naturally occurring carotenoids can be divided into two classes:
 - (1) oxygen-free hydrocarbons, the **carotenes**; and
 - (2) their oxygenated derivatives, the **xanthophylls**.
- The most widespread carotene in the algae is β -carotene (Fig. 1.21).
- There are a large number of different xanthophylls, with the Chlorophyta having xanthophylls that most closely resemble those in higher plants.
- **Fucoxanthin** (Fig. 1.21) is the principal xanthophyll in the golden-brown algae (Chrysophyceae, Bacillariophyceae, Prymnesiophyceae, and Phaeophyceae), giving these algae their characteristic color.
- Like the chlorophylls, the carotenoids are soluble in alcohols, benzene, and acetone but insoluble in water.

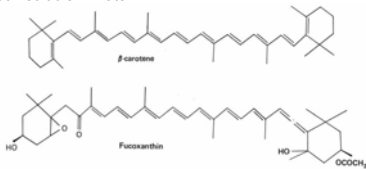


Fig. 1.21 The structure of β -carotene and fucoxanthin.

- 1 Green algae and higher plants use chlorophyll *a/b* binding proteins.
- 2 Brown and golden-brown algae, (diatoms, chrysophytes, dinoflagellates, brown algae, and related groups) use a fucoxanthin chlorophyll *a/c* complex that is an integral part of the thylakoid membrane. The ratio of fucoxanthin to chlorophyll in this complex is approximately 2 : 1 and the characteristic brown or goldenbrown color of these algae is due to the high level of fucoxanthin in these cells. Due to chlorophyll *c* and special xanthophylls, these organisms are especially suited to harvest blue and green light, which are the most abundant at increasing ocean depths. This light harvesting complex also is composed of three membrane-spanning helices and is closely related to the light-harvesting complex in the first group.
- 3 Cyanobacteria, cryptophytes and red algae use the phycobilisome as the major light harvesting complex.

- **Phycobiliproteins** are water-soluble blue or red pigments located on (Cyanophyta, Rhodophyta) or *inside* (Cryptophyta) thylakoids of algal chloroplasts.
- They are described as **chromoproteins** (colored proteins) in which the **prosthetic group** (non- protein part of the molecule) or **chromophore** is a tetrapyrrole (bile pigment) known as **phycobilin**.
- The prosthetic group is tightly bound by covalent linkages to its **apoprotein** (protein part of the molecule).
- Because it is difficult to separate the pigment from the apoprotein, the term **phycobiliprotein** is used.
- There are two different apoproteins, α and β , which together form the basic unit of the phycobiliproteins. To either α or β are attached the colored chromophores.
- The major "blue" chromophore occurring in **phycocyanin** and **allophycocyanin** is **phycocyanobilin**, and the major "red" chromophore occurring in **phycoerythrin** is **phycoerythrobin** (Fig. 1.22).

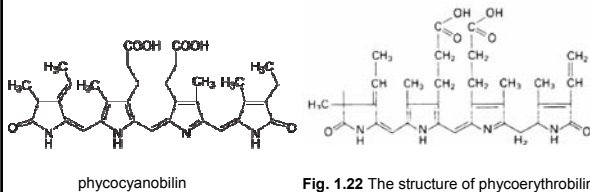
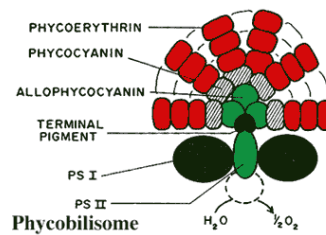
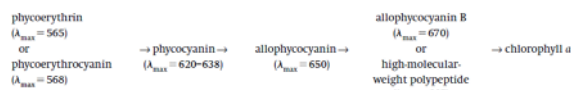


Fig. 1.22 The structure of phycoerythrobin

- The cyanobacteria and chloroplasts of the Rhodophyta and Cryptophyta have evolved membrane-peripheral antenna complexes containing **phycobiliproteins** that transfer light energy to photosystem II reaction centers.
- Like chlorophyll *b/c/d*, the phycobiliproteins expand the range of light energy that can be utilized in photosynthesis.
- Light tends to become blue-green as it courses down the water column, and this light is better absorbed by the biliproteins than chlorophyll *a*.



The pathway of energy transfer is



- In intact cells, the overall efficiency of energy transfer from the phycobilisome to chlorophyll *a* in the thylakoids exceeds 90%.

- The general classification of phycobiliproteins is based on their absorption spectra.
- There are three types of phycoerythrin: R-phycoerythrin and B-phycoerythrin in the Rhodophyta, and C-phycoerythrin in the Cyanophyta.
- There are also three types of phycocyanin: R-phycocyanin from the Rhodophyta and C-phycocyanin and allophycocyanin from the Cyanophyta.
- In addition, in the Cryptophyta there are three spectral types of phycoerythrin and three spectral types of phycocyanin.

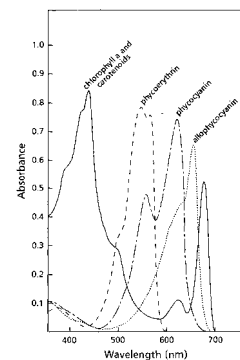


Figure 6-21 Absorption spectra for the phycobilin pigments found in non-chlorophyll *b*-containing cyanobacteria. These accessory pigments extend the range of wavelengths that can be used for photosynthesis, covering wavelengths where neither chlorophyll *a* nor carotenoids show strong absorbances. (Redrawn from Ganett, E. *BioScience* 25:781-788, 1975. © 1975 American Institute of Biological Sciences.)

- **Depriving cells of nitrogen** results in an ordered degradation of phycobilisomes (Fig. 1.25).
- There is a progressive degradation of hexamer rod and linker polypeptides followed by the core peptides. New phycobilisomes are rapidly synthesized on the addition of nitrogen to the medium.
- Phycobilisomes are, thus, an important source of internal nitrogen and offer the algae that have phycobilisomes (cyanobacteria, cryptophytes, and red algae) an important ecological advantage in the open ocean, which is predominantly nitrogen limited.

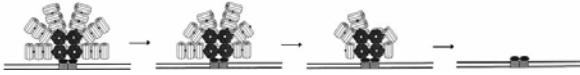


Fig. 1.25 Phycobilisome breakdown under conditions of nitrogen deprivation.

• Chromatic adaptation

Some cyanobacteria can adjust their pigment composition in response to changes in light quality (Fig. 1.24).

- For example, the cyanobacterium *Synechocystis* grown in **green light** produces phycoerythrin (red in color), phycocyanin (blue), and allophycocyanin (blue-green) in a molar ratio of about 2 : 2 : 1; when it is grown in **red light**, the ratio is about 0.4 : 2 : 1.
- The phycobilisome structure changes appropriately, with the peripheral rods having more phycoerythrin hexamers **under green light**, and less phycocyanin hexamers. The allophycocyanin core hexamers stay the same.

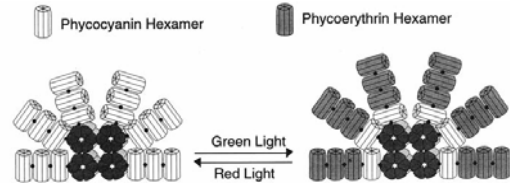


Fig. 1.24 Chromatic adaptation in a phycobilisome of a cyanobacterium.

- **Glycolate**, the major substrate of photorespiration, can be broken down by either **glycolate dehydrogenase** in the mitochondria, or by **glycolate oxidase** in **peroxisomes**, single membrane bounded bodies in the cytoplasm.
- The distribution of the two enzymes is as follows:
 - 1 Glycolate dehydrogenase occurs in the cyanobacteria, cryptophytes, euglenoids, diatoms, and the green algae with the exception of the Charophyceae.
 - 2 Glycolate oxidase occurs in the glaucophytes, red algae, brown algae, and the Charophyceae in the green algae and higher plants.

Mitochondria and peroxisomes

- There are two types of mitochondria in algal cells.
- Mitochondria with **flat lamellae cristae** occur in the red algae, green algae, euglenoids, and cryptophytes (Fig. 1.26).
- Mitochondria with **tubular cristae** occur in heterokonts and haptophytes.

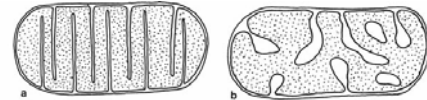
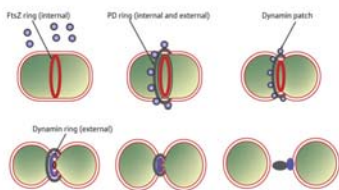


Fig. 1.26 Drawings of the two types of mitochondria that occur in the algae. (a) Mitochondrion with flat lamellar cristae. (b) Mitochondrion with tubular cristae.

- The plastid-dividing ring contracts around the area of plastid fission in association with GTPase proteins called dynamins.
- The PD ring disappears after fission is completed.



Division of chloroplasts and mitochondria

- Chloroplasts and mitochondria divide by pinching in half to form two new organelles.
- A plastid-dividing (PD) ring or mitochondrion-dividing (MD) ring surrounds the organelle in the area of fission (Fig. 1.27).
- Each ring is composed of two parts, an outer ring in the protoplasm outside of the chloroplast and an inner ring in the stroma inside the inner membrane of the chloroplast.
- These rings are also called FtsZ (filamentous temperature-sensitive) rings after a counterpart that is present when bacteria divide.
- The similarity is indicative of the endosymbiotic origin of chloroplasts and mitochondria from bacteria.
- The plastid-dividing ring appears in the area of division and begins to contract after a microbody has migrated to the plastid-dividing ring (Fig. 1.27).

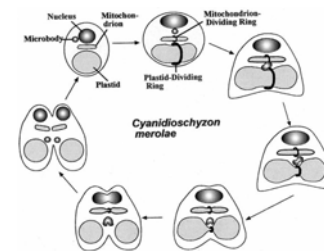
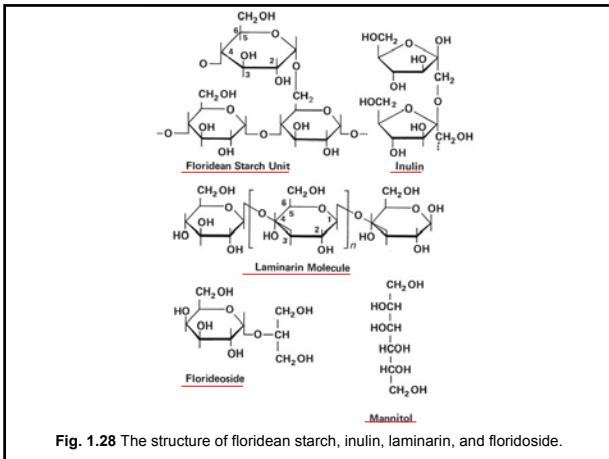


Fig. 1.27 Diagrammatic representation of the behavior of the plastid-dividing ring and mitochondrion-dividing ring in the unicellular red alga *Cyanidioschyzon merolae*.



Storage products

- The storage products that occur in the algae are as follows:
 - High-molecular-weight compounds**
 - 1. α 1,4 Linked glucans**
 - Floridean starch** (Fig. 1.28): This substance occurs in the Rhodophyta and is similar to the amylopectin of higher plants.
 - It stains red-violet with iodine, giving a color similar to that of the stain reaction of animal glycogen.
 - Floridean starch occurs as bowl shaped grains from 0.5 to 25 μm outside the chloroplast, inferring the host in the original endosymbiosis took over formation of storage product.
 - This differs from the Chlorophyta where starch is produced in the chloroplast.
 - Despite the differing locations of starch synthesis, the Rhodophyta and Chlorophyta use a common pathway in the synthesis of starch.

c. Starch: In the Chlorophyta, starch is composed of amylose and amylopectin. It occurs inside the chloroplast in the form of starch grains (Fig. 1.12(e)).

- In the Cryptophyta, starch has an unusually high content of amylose and occurs as grains between the chloroplast envelope and the chloroplast E.R. (Fig. 1.12(b)).
- In the Dinophyta also, starch occurs in the cytoplasm outside of the chloroplast, but its structure is not known.

b. Myxophycean starch: Found in the Cyanophyta, myxophycean starch has a similar structure to glycogen. This reserve product occurs as granules (α granules), the shape varying between species from rod-shaped granules to 25-nm particles to elongate 31- to 67-nm bodies.

b. Chrysolaminarin (leucosin): In the Chrysophyceae, Prymnesiophyta, and Bacillariophyceae, chrysolaminarin consists of β -1,3 linked D-glucose residues with two 1 \rightarrow 6 glycosidic bonds per molecule. Chrysolaminarin occurs in vesicles outside of the chloroplast and has more glucose residues per molecule than laminarin.

c. Paramylon: In the Euglenophyta, Xanthophyceae, and Prymnesiophyta (*Pavlova mesolychnon*), paramylon occurs as water-soluble, single-membrane-bounded inclusions of various shapes and dimensions outside of the chloroplast (Fig. 6.2).

- Paramylon consists solely of β -1,3 linked glucose residues, and the molecule is about as large as that of chrysolaminarin.

- 2. β -1,3 Linked glucans**
 - Laminarin** (Fig. 1.28): In the Phaeophyceae, laminarin consists of a related group of predominantly β -1,3 linked glucans containing 16 to 31 residues.
 - Variation in the molecule is introduced by the number of 1 \rightarrow 6 linkages, the degree of branching, and the occurrence of a terminal mannitol molecule.
 - The presence of a high proportion of C-6 inter residue linkages and of branch points seems to determine the solubility of the polysaccharide in cold water: the greater the number of linkages, the higher the solubility.
 - Laminarin occurs as an oil-like liquid outside of the chloroplasts, commonly in a vesicle surrounding the pyrenoid.

3. Fructosans: *Acetabularia* (Chlorophyta) has an inulin-like storage product consisting of a series of 1,2 linked fructose units terminated by a glucose end group (Fig. 1.28).

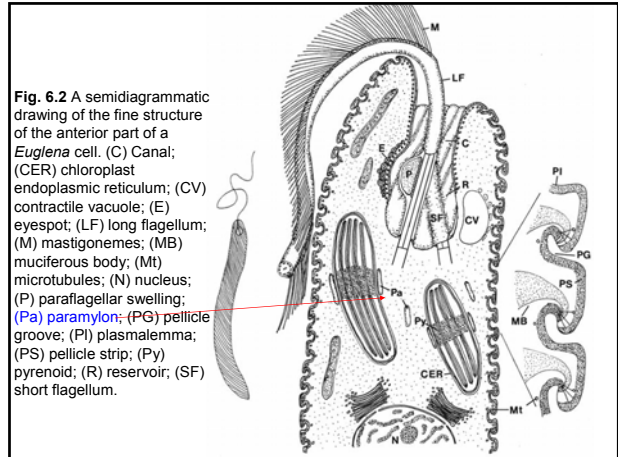
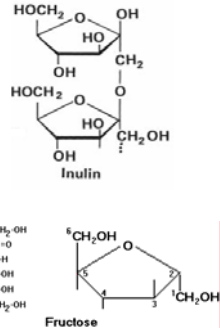


Fig. 6.2 A semidiagrammatic drawing of the fine structure of the anterior part of a *Euglena* cell. (C) Canal; (CER) chloroplast endoplasmic reticulum; (CV) contractile vacuole; (E) eyespot; (LF) long flagellum; (M) mastigonemes; (MB) muciferous body; (Mt) microtubules; (N) nucleus; (P) paraflagellar swelling; (Pa) paramylon; (PG) pellicle groove; (PI) plasmalemma; (PS) pellicle strip; (Py) pyrenoid; (R) reservoir; (SF) short flagellum.

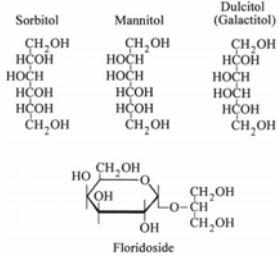
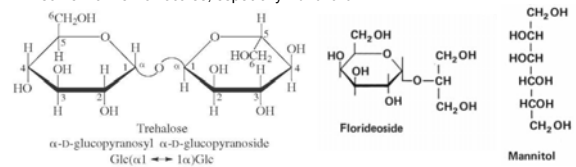


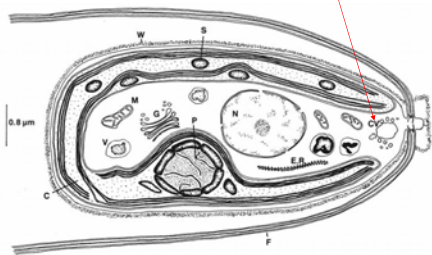
Fig. 4.4 Chemical structure of low molecular polysaccharides that occur in the red algae.

Low-molecular-weight compounds

- 1 Sugars:** Chlorophyta and Euglenophyta form **sucrose** as a reserve product; **trehalose** is found in the Cyanophyta and at low levels in the Rhodophyta.
- 2 Glycosides:** The glycerol glycosides, floridoside (Fig. 1.28) and isofloridoside, are widely distributed in the Rhodophyta.
- 3 Polyols:** Mannitol (Figs. 1.28, 4.4) occurs in Rhodophyta and Phaeophyceae. It is also present in lower green algae, where it replaces sucrose as a photosynthetic product. Free glycerol occurs widely in the algae and is an important photosynthetic product in several zooxanthellae (endosymbiotic algae in animals) and in some marine Volvocales, especially *Dunaliella*.



- Most algal flagellates have two contractile vacuoles in the anterior end of a cell (Fig. 1.1).



Contractile vacuoles

- The ability of algal cells to adjust to changes in the salinity of the medium is an important aspect of the physiology of these cells.
- In cells with walls, this osmoregulation is accomplished with the aid of turgor pressure, whereas in naked cells it is accomplished by means of
 - contractile vacuoles and/or
 - regulation of the solutes present in the cells.
- In the latter case, cells increase the internal concentration of osmotically active molecules and ions when the concentration of dissolved solutes increases in the external medium.
- Like wise, the internal concentration of such molecules decreases when the concentration of dissolved salts in the external medium decreases.

- The contractile vacuoles of the Cryptophyta are characteristic of the algae (Fig. 1.29).
- In the Cryptophyta, the contractile vacuole occurs in a fixed anterior position next to the flagellar depression. At the beginning of the filling phase (**diastole**), there is no distinct contractile vacuole, only a region filled with small (ca. 0.5- μ m diameter) **contributory vacuoles**.
- These vacuoles fuse to form a large irregular vacuole which subsequently rounds up.
- The contributory vacuoles destined to form the next contractile vacuole now appear around the rounded contractile vacuole.
- The contractile vacuole fuses with the plasma membrane of the flagellar pocket and discharges its contents outside the cell. The area of the plasma membrane that fuses with the contractile vacuole does not have a periplast (specialized plates within the plasma membrane). This area is, instead, bounded by microtubules.
- The membrane of the contractile vacuole is recovered by the cell as small vesicles with an electron-dense coat, and the membrane components are reutilized by the cell.
- These vesicles plus the contractile vacuole occur in the **spongiome** or area around the contractile vacuole.

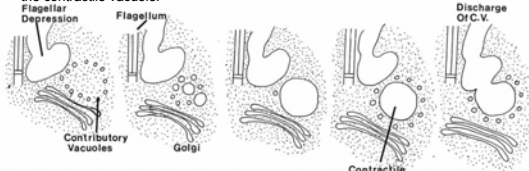


Fig. 1.29 Semidiagrammatic illustration of the behavior of the contractile vacuole (C.V.) complex during filling and discharge in the Cryptophyta.

- A contractile vacuole will fill with an aqueous solution (**diastole**) and then expel the solution outside of the cell and contract (**ystole**).
- The contractile vacuole rhythmically repeats this procedure.
- If there are two contractile vacuoles, they usually fill and empty alternately.
- Contractile vacuoles **occur more frequently in fresh water** than marine algae, a phenomenon that gives credence to the theory that the contractile vacuoles maintain a water balance in the cells.
- The algal cells in fresh water have a higher concentration of dissolved substances in their protoplasm than in the surrounding medium so that there is a net increase of water in the cells. The contractile vacuoles act to expel this excess water.
- An **alternate theory** on the function of the contractile vacuoles is that they remove waste products from the cells.
- The Dinophyta have a structure similar to a contractile vacuole, called a **pusule**, which may have a similar function but is more complex.

Nutrition

- Algae can be either **autotrophic (lithotrophic or holophytic)** or **heterotrophic (organotrophic)** (Table 1.1).
- **Autotrophic algae** use inorganic compounds as a source of carbon. Autotrophs can be **photoautotrophic (photolithotrophic)**, using light as a source of energy, or **chemoautotrophic (chemolithotrophic)**, oxidizing inorganic compounds for energy.
- **Photoautotrophs** Algae depend entirely upon their photosynthetic apparatus for their metabolic necessities, using sunlight as the source of energy, and inorganic CO₂ as the carbon source to produce carbohydrates and ATP.

Table 1.1 | Types of nutrition found in the algae

Type of nutrition	Principle source of energy for growth	Principal source of carbon for growth
<i>Autotrophic</i>		
Photoautotrophic	Light	Carbon dioxide
Chemoautotrophic	Oxidation of organic compounds	Carbon dioxide
<i>Heterotrophic</i>		
Photoheterotrophic	Light	Organic compounds
Chemoheterotrophic	Oxidation of organic compounds	Organic compounds

- In fresh water algae the contractile vacuole cycle lasts for 4 to 16 seconds, whereas in marine species the cycle can last for up to 40 seconds.
- Algal flagellates use a combination of contractile vacuoles and osmoregulation to control the water content of their cells.
- In the chrysophyte *Poterioochromonas malhamensis* (*Ochromonas malhamensis*), the internal level of isofloridoside (α -D-galactopyranosyl-1 \rightarrow 1-glycerol) is proportional to the external osmotic value as long as the external solute concentration exceeds 75 mOsm.
- Below this external solute concentration, the influx of water into the cytoplasm is counter balanced by means of the contractile vacuoles.

- **Auxotrophic Algae** Some algae, particularly the flagellates, are **auxotrophic**, requiring a small amount of an organic compound, but not as an energy source. These algae cannot synthesize these essential components such as vitamins (biotin, thiamine, cobalamin = B12) and have to import them.
- **Mixotrophy** it is a combination of different nutritional strategies of photoautotrophy, auxotrophy and heterotrophy.
- The relative contribution of autotrophy and heterotrophy to growth within a mixotrophic species **varies along a gradient** from algae whose dominant mode of nutrition is phototrophy, through those for which phototrophy or heterotrophy provides essential nutritional supplements, to those for which heterotrophy is the dominant strategy.
- The degree of mixotrophie in chlorophyll-containing algae **varies with environmental conditions** (light, prey abundance). For example, heterotrophy is important for the acquisition of carbon when light is limiting and, conversely, autotrophy maintains a cell during periods when particulate food is scarce.

- **Heterotrophic algae** use organic compounds for growth. Heterotrophs can be
 - **photoheterotrophs (photoorganotrophs)**, using light as a source of energy and organic compounds as principle source of carbon for growth, or
 - **chemoheterotrophs (chemoorganotrophs)**, oxidizing organic compounds for energy.
- Heterotrophic algae may be
 - **phagocytotic (holozoic)**, engulfing **food particles** such as bacteria and other cells as particulate prey into food vesicles for digestion, or they may be
 - **osmotrophic**, absorbing **nutrients in a soluble form** through the plasma membrane.
 - If the algae live heterotrophically on dead material, they are **saprophytic**;
 - if they live off a live host, they are **parasitic**.

Algal systematics and gene sequencing

- No easily definable classification system acceptable to all exists for algae because taxonomy is under constant and rapid revision at all levels following every day new genetic and ultrastructural evidence.
- The systematic arrangement of algae into Divisions or Phyla, and Classes is based on basic traits, such as
 - the chemical composition of photosynthetic pigments,
 - storage substances that accumulate,
 - type of cell wall, and
 - cytological characters like cellular ultrastructure, especially the characteristics of chloroplasts and their endosymbiotic origin.
- Recently, classifications have been supported by molecular genetics.

- On the basis of their nutritional strategies, **mixotrophic** algae are classified into four groups:
 - Obligate heterotrophic algae.** They are primarily heterotrophic, but are capable of sustaining themselves by phototrophy when prey concentrations limit heterotrophic growth.
 - Obligate phototrophic algae.** Their primary mode of nutrition is phototrophy, but they can supplement growth by phagotrophy and/or osmotrophy when light is limiting.
 - Facultative mixotrophic algae.** They can grow equally well as phototrophs and as heterotrophs.
 - Obligate mixotrophic algae.** Their primary mode of nutrition is phototrophy, but phagotrophy and/or osmotrophy provides substances essential for growth (photoautotrophic algae can be included in this group).
- Most algal divisions contain mixo- or heterotrophic species. Some chlorophyll-containing species can even lose their pigments when living heterotrophic

- 1 Eukaryotic ribosomes** (Fig. 1.30). The large 60S subunit contains 28S, 5.8S, and 5S rRNAs, and 49 proteins. The small 40S subunit contains 18S rRNA and 33 proteins.
- 2 Prokaryotic ribosomes.** The large 70S subunit contains 5S and 23S rRNAs as well as 34 ribosomal proteins. The small 30S subunit contains a single 16S rRNA and 21 proteins.
- 3 Mitochondrial ribosomes.** These are similar, although not the same, as prokaryotic ribosomes. They are not used to produce algal phylogenies, mostly because mitochondria have been transferred between eukaryotic hosts and, therefore, do not reflect the evolutionary history of the organism.

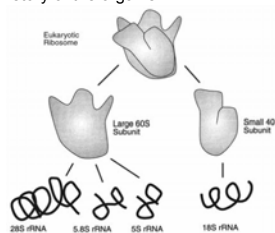
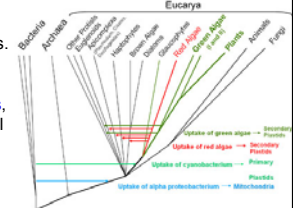


Fig. 1.30 The components of a eukaryotic ribosome.

Gene sequencing

- Each species has differences in the nucleotides that make up the DNA and differences in nucleotides that can be used to produce an evolutionary history of the cell.
- The DNA nucleotides that are most commonly sequenced to produce phylogenies are those of ribosomal DNAs (rDNAs).
- These rDNA nucleotides make up the genes that code for the rRNAs.
- rRNAs occur in ribosomes and there are **three types of ribosomes**, each made up of a large and small subunit:



- The **rDNA** for the **5S rRNA** has been also used in phylogeny studies. Although less nucleotides are in the rDNA coding for 5S rRNA, making it easier to sequence, the data have been suspect because of large deviations in the nucleotides.
- The DNA coding for **other molecules**, such as ribulose biphosphate carboxylase/oxygenase and actin have also been used in determining phylogeny.

- The **rDNA** for the **18S rRNA** of the small subunit of the eukaryotic ribosome is the form of rDNA **usually sequenced** to determine the phylogeny of eukaryotic organisms.
- The nucleotides coding for all of the ribosomal subunits are encompassed within a single operon* and transcribed by a single RNA polymerase.
- The procedure for determining the nucleotide sequences is available in any basic biochemistry book.

*:In genetics, an operon is a functioning unit of genomic DNA containing a cluster of genes under the control of a single promoter. A promoter is a region of DNA that initiates transcription of a particular gene. Promoters are located near the transcription start sites of genes, on the same strand and upstream on the DNA (towards the 5' region of the sense strand). Promoters can be about 100–1000 base pairs long.

Classification

- There are four distinct groups within the algae.
- **1 Prokaryotes** ***. The cyanobacteria are the only prokaryotic algae.
- **2 Eukaryotic algae** with chloroplasts surrounded by the two membranes of the chloroplast envelope.
- **3 Eukaryotic algae** with the chloroplast surrounded by one membrane of chloroplast endoplasmic reticulum.
- **4 Eukaryotic algae** with the chloroplast surrounded by two membranes of chloroplast endoplasmic reticulum.

- *** At one time, the occurrence of chlorophyll *b* in cyanobacteria was used as a criterion to place the organisms in a separate group, the **Prochlorophyta**. Modern nucleic-acid sequencing, however, has shown that chlorophyll *b* evolved a number of times within the cyanobacteria and the term Prochlorophyta has been discarded

- Gene sequencing has been the most active field of phylogenetic systematics in the last decade and has provided important new information on the relationships between algae. However, as stated by Manhart and McCourt (1992): . . . **molecular data are not a magic bullet for species problems. They are data, no more, no less. Some molecular data are informative, and others are misleading. Molecular data are fraught with many of the same difficulties as morphological data . . .**

- **Group 1 Prokaryotic algae**
- **Cyanophyta** (cyanobacteria): chlorophyll *a*; phycobiliproteins.
- **Group 2 Eukaryotic algae** with chloroplasts surrounded only by the two membranes of the chloroplast envelope.
- **Glaucophyta**: algae that represent an intermediate position in the evolution of chloroplasts; photosynthesis is carried out by modified endosymbiotic cyanobacteria.
- **Rhodophyta** (red algae): chlorophyll *a*; phycobiliproteins; no flagellated cells; storage product is floridean starch.
- **Chlorophyta** (green algae): chlorophylls *a* and *b*; storage product, starch, is found inside the chloroplast.

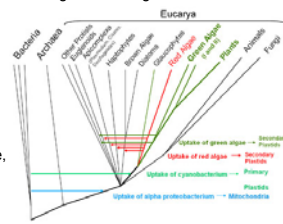
- The standard botanical classification system is used in the systematics of the algae:
- Phylum – phyta
- Class – phyceae
- Order – ales
- Family – aceae
- Genus
- Species

- **Group 4 Eukaryotic algae** with chloroplasts surrounded by two membranes of chloroplast endoplasmic reticulum.
- **Cryptophyta** (cryptophytes): nucleomorph** present between inner and outer membrane of chloroplast endoplasmic reticulum; starch formed as grains between inner membrane of chloroplast endoplasmic reticulum and chloroplast envelope; chlorophyll *a* and *c*; phycobiliproteins; periplast inside plasma membrane.
- **Heterokontophyta** (heterokonts): anterior tinsel and posterior whiplash flagellum; chlorophyll *a* and *c*; fucoxanthin; storage product usually chrysolaminarin occurring in vesicles.

** **Nucleomorphs** are small, vestigial eukaryotic nuclei found between the inner and outer pairs of membranes in certain plastids. They are thought to be vestiges of primitive red and green algal nuclei that engulfed a prokaryote (plastid).

- **Group 3 Eukaryotic algae** with chloroplasts surrounded by one membrane of chloroplast endoplasmic reticulum.
- **Euglenophyta** (euglenoids): chlorophylls *a* and *b*; one flagellum with a spiraled row of fibrillar hairs; proteinaceous pellicle in strips under the plasma membrane; storage product is paramylon; characteristic type of cell division.
- **Dinophyta** (dinoflagellates): mesokaryotic nucleus; chlorophylls *a* and *c*₁; cell commonly divided into an epicone and a hypococone by a girdle; helical transverse flagellum; thecal plates in vesicles under the plasma membrane.
- **Apicomplexa**: heterotrophic flagellates with colorless plastids.

- Data from molecular studies indicate that the red algae diverged about 1400 million years ago from the common line leading to higher plants.
- This was followed by divergence of the green algae and, then, multiple independent secondary endosymbioses evolving to those algae with chloroplast endoplasmic reticulum.
- The host phagocytic organisms leading to the euglenoids was probably a kinetoplastid*, that leading to the dinoflagellates was probably an apicomplexan**, and that leading to the photosynthetic cryptophytes and haptophytes was a colorless cryptophyte and haptophyte, respectively.
- The host organisms leading to the heterokonts have not been identified



- * Kinetoplastida (or Kinetoplastea, as a class) is a group of flagellated protists belonging to the phylum Euglenozoa, and characterised by the presence of an organelle called kinetoplast (hence the name).
- ** The Apicomplexa (also called Apicomplexia) are a large superphylum of parasitic protists. Most of them possess a unique form of organelle that comprises a type of plastid called an apicoplast, and an apical complex structure. The organelle is an adaptation that the organism applies in penetration of a host cell.

- Chrysophyceae** (golden-brown algae)
- Synurophyceae**
- Eustigmatophyceae**
- Pinguicophyceae**
- Dictyochophyceae** (silicoflagellates)
- Pelagophyceae**
- Bolidophyceae**
- Bacillariophyceae** (diatoms)
- Raphidophyceae** (chloromonads)
- Xanthophyceae** (yellow-green algae)
- Phaeothamniophyceae**
- Phaeophyceae** (brown algae)
- Prymnesiophyta** (haptophytes): two whiplash flagella; haptonema present; chlorophyll a and c; fucoxanthin; scales common outside cell; storage product chrysolaminarin occurring in vesicles.

Other Classification method

- one phylum of prokaryotic algae, Cyanophyta, and
- ten phyla of eukaryotic algae: Glaucophyta, Chlorarachniophyta, Euglenophyta, Dinophyta, Cryptophyta, Haptophyta, Ochrophyta, Rhodophyta, Chlorophyta and Charophyta.

Table 1. Classification scheme of different algal groups.

Kingdom	Phylum	Subphylum	Class
Prokaryota	Cyanophyta		Cyanophyceae
Eukaryota	Chlorophyta	Chlorophytina	Chlorophyceae
			Chlorophytina
			Chlorophytina
			Chlorophytina
			Chlorophytina
			Chlorophytina
			Chlorophytina
			Chlorophytina
			Chlorophytina
			Chlorophytina
Chlorophyta	Chlorophytina	Chlorophytina	Chlorophyceae
			Chlorophyceae
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			Chlorophyceae
			Chlorophyceae
			Chlorophyceae
			Chlorophyceae
Chlorophyta	Chlorophytina	Chlorophytina	Chlorophyceae
			Chlorophyceae
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			Chlorophyceae
			Chlorophyceae
			Chlorophyceae
			Chlorophyceae
			Chlorophyceae

Other Classification method

- A tentative scheme of classification is adopted mainly based on the work of Van Den Hoek et al. (1995) and compared with the classifications of Bold and Wynne (1978), Margulis et al. (1990), Graham and Wilcox (2000), and South and Whittick (1987).
- Prokaryotic members of this assemblage are grouped into two divisions: Cyanophyta and Prochlorophyta, whereas
- eukaryotic members are grouped into nine divisions: Glaucophyta, Rhodophyta, Heterokontophyta, Haptophyta, Cryptophyta, Dinophyta, Euglenophyta, Chlorarachniophyta, and Chlorophyta (Table 1.1).

TABLE 1.1 Classification Scheme of the Different Algal Groups

Kingdom	Division	Class
Prokaryota	Cyanophyta	Cyanophyceae
		Prochlorophyta
Eukaryota	Glaucophyta	Glaucophyceae
		Rhodophyta
	Heterokontophyta	Bacillariophyceae
		Chrysophyceae
		Xanthophyceae
		Eustigmatophyceae
		Bacillariophyceae
		Raphidophyceae
		Dictyochophyceae
		Phaeophyceae
		Haptophyta
	Cryptophyta	
	Euglenophyta	Euglenophyceae
		Chlorarachniophyta
		Chlorophyta
	Chlorophyta	Prasinophyceae
		Chlorophyceae
		Ulvophyceae
Cladophorophyceae		
Bryopsidophyceae		
Zygnematales		
Trentepohliophyceae		
Klebsormidiophyceae		
Charophyceae		
Dasycladophyceae		

- When the cyanobacteria evolved, the atmosphere contained little or no oxygen and was composed primarily of methane (CH₄), ammonia (NH₃), and other reduced compounds.
- Photosynthesis by the cyanobacteria eventually built up the oxygen content of the atmosphere to what it is today (20%).
- The first eukaryotic algae appeared in a form similar to the extant Glaucophyta, with endosymbiotic cyanobacteria instead of chloroplasts.
- It is difficult to fix this date exactly because these first algae were composed of soft tissues and would not have been preserved.

Algae and the fossil record

- The cyanobacteria are the oldest group of algae with definite fossil remains in the form of stromatolites (Fig. 2.53), dating back about 2700 million years.



Fig. 2.53 Cyanobacterial stromatolites in the process of formation in Shark Bay, Western Australia.

Table 1.2 First appearance of algae in the geological time scale

Era	Period	Epoch	Millions of years ago	First appearance of algal fossil
Cenozoic	Quaternary	Holocene	1.8	
		Pleistocene	5.5	
	Tertiary	Pliocene	5.5	
		Miocene	25.0	Xanthophyta
		Oligocene	36.0	
		Eocene	53.5	Euglenophyta
Mesozoic		Palaeocene	65.0	
Mesozoic	Cretaceous		135	Chrysophyta
			191–205	
	Jurassic		235–245	Bacillariophyta
Paleozoic	Permian		275–290	Phycomycophyta
			360–380	
	Carboniferous		405–430	
	Devonian		435–460	Stoneworts (Chlorophyta)
	Silurian		500–530	
Proterozoic	Precambrian		570–610	
			3000	Cyanophyta, Rhodophyta, Chlorophyta

- In order to appear in the fossil record, algae would usually have to be large or to have some calcified (CaCO_3) or silicified (SiO_2) structures, which are preserved in sedimentary rocks.
- The appearance of fossil members of the algal classes in the geological timetable is presented in Table 1.2. This table does not purport to show when the algal groups first evolved, but shows only where fossil specimens appear in the geological timetable.

- Red and green algae fossils resembling existing species have been dated at about 600 million years ago, by the end of Precambrian. These algae are well preserved due to their calcium carbonate deposits.
- The green algae of the order Dasycladales are the most abundant macroscopic fossil algae from early Cambrian, in which the number of fossil genera is larger than the number of living genera.
- Coccoliths (haptophytes) with calcified walls, and diatoms with silicified skeletons, are found in Mesozoic sediments.
- Marine diatoms formed large Cretaceous deposits known as diatomaceous earth, reaching thicknesses of several hundred meters.
- Fossil dinoflagellates are known from the Silurian, 450 million years ago. Hundreds of species of dinoflagellates and diatoms that have been described are now extinct.
- Other groups of algae are not abundant in fossil records.